

## Natural history and description of the dendrolimnetic larva of *Coryphagrion grandis* (Odonata<sup>1</sup>)

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Received 07 May 2001; revised and accepted 28 November 2001.

Key words: Odonata, dragonfly, Zygoptera, larva, evolution, Gondwana, East Africa, phytotelmata.

### Abstract

The morphology of the last stadium larvae of the African *Coryphagrion grandis* is described for the first time, based on one exuvia and three last instar larvae from Kenya. Taxonomically important morphological characters are illustrated and discussed. Important characters are the shape of the larval caudal appendages, the labial palpi and the branched setae on the inner side of tibiae and tarsi. Notes on habitat conditions are given and compared with results for other odonate species, which are known to breed in phytotelmata. The systematic position of *Coryphagrion* is briefly discussed. *Coryphagrion* is hypothesised to be phylogenetically closely related with the neotropical family Pseudostigmatidae based on larval morphology, adult morphology, behaviour and ecology.

### Introduction

In tropical habitats world-wide at least 24 genera and 47 species of odonates are known to breed in phytotelmata, with the Zygoptera being the majority (Corbet 1999). In the afrotropical region only larvae of three species have been recorded from phytotelmata so far: *Coryphagrion grandis* Morton (Lounibos 1980), *Hadrothemis camarensis* Kirby (Copeland et al. 1996) and *H. scabifrons* (Ris) (Corbet & McCrae 1981).

It had been long anticipated, that *C. grandis* breeds in phytotelmata "like the tropical American pseudostigmatids" (Pinhey 1962: 23). In 1960 the first observation of a female laying eggs in a "toadstool full of water, high up in a tree" was reported (Pinhey 1962). The first report of a successful reproduction of *C. grandis* in phytotelmata was made by Lounibos (1980), who collected a larva from tree holes from the Kombeni Forest, Rabai, Kenya.

The systematic position of the monotypic *C. grandis* is still unclear. According to the original description (Morton 1924) and many catalogues and checklists (Davies & Tobin

<sup>1</sup> The species has been assigned to the family Megapodagrionidae so far; This is unlikely in the light of new findings which are outlined in this paper. A final family assignment depends on the results of the ongoing investigation of imaginal characters.

1984; Tsuda 1991; Bridges 1994) *Coryphagrion* belongs to the Megapodagrionidae. Bechly (1996) considered the taxon *Coryphagrion* as a sistergroup (Coryphagrionidae) to the neotropical Pseudostigmatidae, based on wing venational autapomorphies, size and oviposition mode. Similarly in a phylogenetic analysis of higher level relationships in Odonata *Coryphagrion* clustered together with all genera of the neotropical Pseudostigmatidae, but was very distant from all genera belonging to the Megapodagrionidae (A. Rehn 1999, oral presentation, WDA symposium, July 11-16, Colgate University, Hamilton NY USA).

Up to now, information on larval structures and natural history of *C. grandis* are practically non-existent. The paper presents larval characters and notes on habitat conditions.

## Material and methods

### *Collection sites*

Coastal forests in Kenya were visited 08 April - 24 May 2000, 10-21 December 2000 and 18 March - 15 April 2001. Collecting and observations on *Coryphagrion grandis* were done in the Arabuko-Sokoke Forest (03°11-29'S, 39°48'-40°00'E), Muhaka Forest (04°19'S, 39°31'E), Buda Forest (04°26-27'S, 39°23-25'E), Gongoni Forest (04°23-25'S, 39°27-29'E) and different forest areas, e.g. Makadara and Mwele Forest in the Shimba Hills (04°09-20'S, 39°16-30'E).

In some of these forests, e.g. Muhaka Forest, Gongoni Forest and in large parts of the Arabuko Sokoke Forest no permanent water sources are available. The only water sources are seasonal pools and water-filled treeholes, with the latter filling up very quickly and keeping the water longer than the seasonal pools.

### *Habitat conditions*

The height, width, circumference, depth and water volume of the treeholes were measured and presence or absence of larvae were recorded. All larvae were measured; presence of other dragonfly larvae, i.e. *Hadrothemis scabrifrons*, freshwater crabs and the number of mosquitoes were recorded. Measurements of the water pH, oxygen content and conductivity were taken with digital instruments from Heindl.

### *Morphological descriptions*

The description of the last instar larva is based on one exuvia of a female emerged in captivity, three preserved final stadium larvae (1 ♂, 2 ♀) and 19 intermediate stadia; all V. Clausnitzer leg. 08 April - 24 May 2000, 10-21 December 2000. All larvae were preserved in 70% alcohol after collection. The exuvia and final instar larvae were measured and drawn, using a stereomicroscope; measurements were determined to the nearest 0.1 mm using an eyepiece micrometer. One larva was dissected in ethanol for scanning electron microscopy. Preparations were critical point dried, sputter-coated with gold and examined in a Hitachi S-800 scanning electron microscope.

## Results

### Notes on habitat

Table 1 shows measurements on the water chemistry of treeholes. Unfortunately the preceding dry season in 2001 was extraordinary dry, so that measurements could be taken from four treeholes only.

Table 1. pH, oxygen content, oxygen saturation (water temperature 25°C) and conductivity from tree holes in the Shimba Hills NP (04°12'S, 39°27'E), 367 m a.s.l., 30 March 2001.

height (m)	circumference (cm)	depth (cm)	water vol. (l)	pH	oxygen content (mg/l)	oxygen saturation (%)	conductivity ( $\mu$ S)
1.60	55	21	1.80	6.2	1.0	12.1	>2,000
1.00	31	55	5.00	6.6	0.6	07.3	860
0.40	15	05	0.08	6.1	1.3	15.7	790
0.25	37	41	1.20	6.4	0.5	06.0	>2,000

65% of all surveyed phytotelmata ( $n = 75$ ) in different coastal forests in Kenya were occupied by larvae of *Coryphagrion grandis* and/or *Hadrothemis scabrifrons* (Table 2), in most cases only one larva was present (Fig. 1). In a few cases several larvae of one and of different cohorts were found in larger treeholes with a lot of detritus, e.g. in the Shimba Hills (3 l water vol.) six larvae of *C. grandis* (3 larvae: 0.25 cm, 1 larva: 0.49 cm, 1 larva 0.87 cm, 1 larva 0.90 cm, all measurements excluding lamellae) were found in on 09 May 2000. The average tree holes were comparatively small and only a few extremely large treeholes were found in the forests (Table 2). A more detailed description of coastal forests is given in Clausnitzer (2002).

Table 2. Median and range (in brackets) of physical parameters of tree holes in different forests, percentage of tree holes with larvae of *Coryphagrion grandis* (*C. g.*) and *Hadrothemis scabrifrons* (*H. s.*) and mean number of *C. grandis* larvae per tree hole; ASF: Arabuke Sokoke Forest, Shimba 1: Makadara Forest, Shimba 2: Badas.

locality	$n$	vol. l	height (m)	diameter (cm)	% <i>C. g.</i>	% <i>H. s.</i>	mean <i>C. g.</i>
ASF	28	0.50 (0.007-1.40)	0.3 (0.2-1.1)	7.5 (2.0-19.0)	53.6	10.7	0.9 $\pm$ 1.3
Buda	9	0.40 (0.030-0.95)	0.7 (0.2-1.6)	5.0 (3.0-10.0)	77.8	0.0	1.2 $\pm$ 0.9
Gongoni	18	0.25 (0.120-0.36)	0.0 (0.0-1.6)	7.0 (4.5-09.5)	44.4	27.7	0.4 $\pm$ 0.5
Shimba 1	4	0.13 (0.090-0.35)	0.8 (0.6-2.0)	5.0 (4.8-06.0)	70.0	10.0	0.5 $\pm$ 0.6
Shimba 2	6	0.75 (0.080-5.00)	0.7 (0.3-2.0)	8.8 (4.5-30.0)	70.0	10.0	2.3 $\pm$ 2.9
Muhaka	10	0.80 (0.060-4.00)	0.8 (0.2-1.5)	5.5 (3.0-100.0)	60.0	20.0	0.7 $\pm$ 0.8

The presence of *C. grandis* larvae were significantly correlated with water depth (Spearman rank correlation coefficient: 0.4498,  $n = 76$ ,  $p < 0.000$ ) and water volume (Spearman rank correlation coefficient: 0.4489,  $n = 76$ ,  $p < 0.000$ ). The mean value for phytotelmata with *C. grandis* larvae was 0.72 litre ( $n = 50$ , range 0.06-5), for phytotelmata without larvae 0.21 ( $n = 26$ , range 0.007-1.4). It has to be noted that phytotelmata included rain water filled coconut shells on the forest floor (Gongoni Forest, Table 3). There were no significant correlations between the number of *C. grandis* larvae and height of phytotelmata (Spearman rank correlation coefficient: 0.1588,  $n = 76$ ,  $p = 0.171$ ), phytotelmata diameter (Spearman rank correlation coefficient: 0.2433,  $n = 76$ ,  $p = 0.034$ ) or circumference of phytotelmata (Spearman rank correlation coefficient: 0.2570,  $n = 76$ ,  $p = 0.025$ ).

Table 3. Presence or absence and size of dragonfly larvae (*C. g.*= *Coryphagrion grandis*, *H. s.* = *Hadrothemis scabrifrons*), number of mosquitoes and water volume (l) in coconut shells on the ground of the Gongoni Forest, Kenya, 11 May 2000; only one larva of either species was found per coconut shell.

I	0.12	0.16	0.16	0.18	0.20	0.21	0.25	0.25	0.26	0.29	0.29	0.31	0.32	0.32	0.34	0.41
Mosquitoes	13	12	17	22	8	11	34	9	22	7	8	4	4	29	7	42
<i>H. s.</i> (mm)	-	-	-	-	-	10.4	-	-	2.1	3.1	-	12.1	13.0	-	-	-
<i>C. g.</i> (mm)	3.2	6.4	-	-	6.2	-	-	5.5	-	4.8	5	-	-	-	7.4	-

*Description of the ultimate stadium larva*

Figure 2a gives the general habitus of the *C. grandis* larva, Table 4 shows measurements on typical larval features based on the examination of three larvae and one exuvia.

The antennae are 7-segmented (Fig. 3a), as long as the head, with few scattered setae. The pedicellus is about 1.6 to 1.8 times as long as scapus. The postocular region bears spine shaped setae.

The mandibles (Fig. 3d) are armed with four outer teeth (external branch), which are connected to a pointed lateral tooth (ventral branch) and two inner teeth (internal branch). The lacinia of the maxilla is provided with six slightly curved and strong teeth; the simple galea is covered with long setae.

The larvae have a prementum with numerous short setae (Fig. 3b); each labial palp is provided with six, seven or eight palpal setae, shorter or even in length as the movable hook. In addition to the movable hook, one blunt teeth and one acute end hook are located on the distal margin of the labial palpi (Fig. 3b)

Most setae on the legs are simple-pointed spine-like setae, the others are branched. Figure 4a shows the number and arrangement of the branched setae of the tibiae and tarsi. The branched setae are not randomly arranged, they are only found on the distal third of the ventrolateral side of the tibiae (Fig. 5a) and on the inner side of tarsi

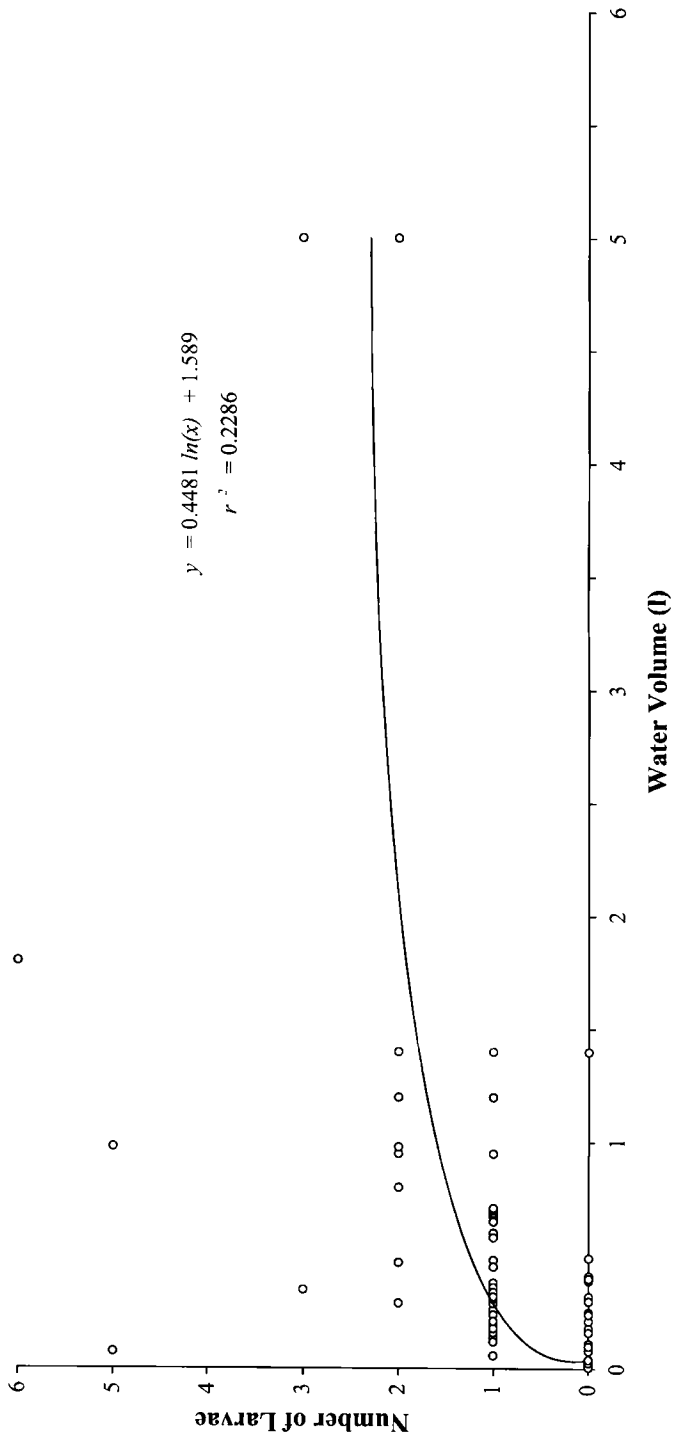


Figure 1. The log-linear relation between the number of dragonfly larvae (*Coryphagtrion grandis* or *Hadrothemis scabifrons*) in phytotelmata of different Kenyan coastal forests and water volume (l);  $n = 76$ .

Table 4. Measurements of last stadium larvae of *Coryphagrion grandis* (mm), ASF: Arabuke Sokoke Forest.

	♀ 1 exuvia	♀ 2 larva	♂ 1 larva	♂ 2 larva
Collection site	Shimba Hills	Shimba Hills	ASF	Shimba Hills
Date	18 xii 2000	15 v 2000	22 xii 2000	15 v 2000
Body length	23.2	15.9	19.7	- *
Antenna length	4.1	3.3	2.8	- **
Head width	5.6	5.3	5.1	5.3
Caudal appendages length (lateral/median)	3.6/3.9	3.5/-	3.3/3.0	3.5/3.6
Praementum length	4.2	4.0	3.4	3.4
Leg length (femur/tibia/tarsi)				
- prothoracal	3.4 / 4.4 / 1.6	2.6 / 3.6 / 1.4	2.6 / 3.6 / 1.1	2.9 / 3.8 / 1.4
- mesothoracal	4.4 / 4.7 / 1.9	3.6 / 4.2 / 1.5	3.5 / 4.0 / 1.4	3.8 / 4.5 / -
- metathoracal	5.6 / 6.0 / 2.2	4.8 / 4.6 / 1.8	4.7 / 4.9 / 1.7	4.8 / 5.2 / 1.8
Wing sheath length (Fw/Hw)	9.5 / 9.2	9.1 / 8.4	8.3 / 7.8	8.5 / 8.0

\* strongly stretched abdomen  
\*\* missing antennomeres

(Fig. 5b). The highest density is located at the distal end of the tibiae (Fig. 5a). Altogether there are up to approximately 250 branched setae on one hind leg, a little lesser on the prothoracal and mesothoracal legs.

Mostly branched setae arise from distally oriented sockets. On the tibiae there are only branched setae with three points (Fig. 5a), while on the tarsi there are also branched setae with more points or feathered forms (Figs 4b, 5b). However, multiply branched setae with more than three points are less frequently than three-pointed setae.

The hind wing sheaths reach to the posterior end of S7 in females and the end of S5 in males. The reason for this difference is the developing secondary copulatory apparatus in males and entailing room requirements. For instance, the second abdominal segment of male 1 is 1.9 mm long, while the second segment of female 2 is only 1.1 mm long. Correspondingly female wing sheaths cover more abdominal segments than male wing sheaths in last stadium larvae.

Female gonapophysis extending to the posterior border of S10 (Figs 2b, 2c); male gonopods as in Figure 2e.

The larval caudal appendages are stalked at the base and spatulate distally (Figs 2d, 6). The dorsal side of the stalked part of the median appendage and the lateral part of the stalked part of the lateral appendages are provided with many piliform setae.

*Behaviour*

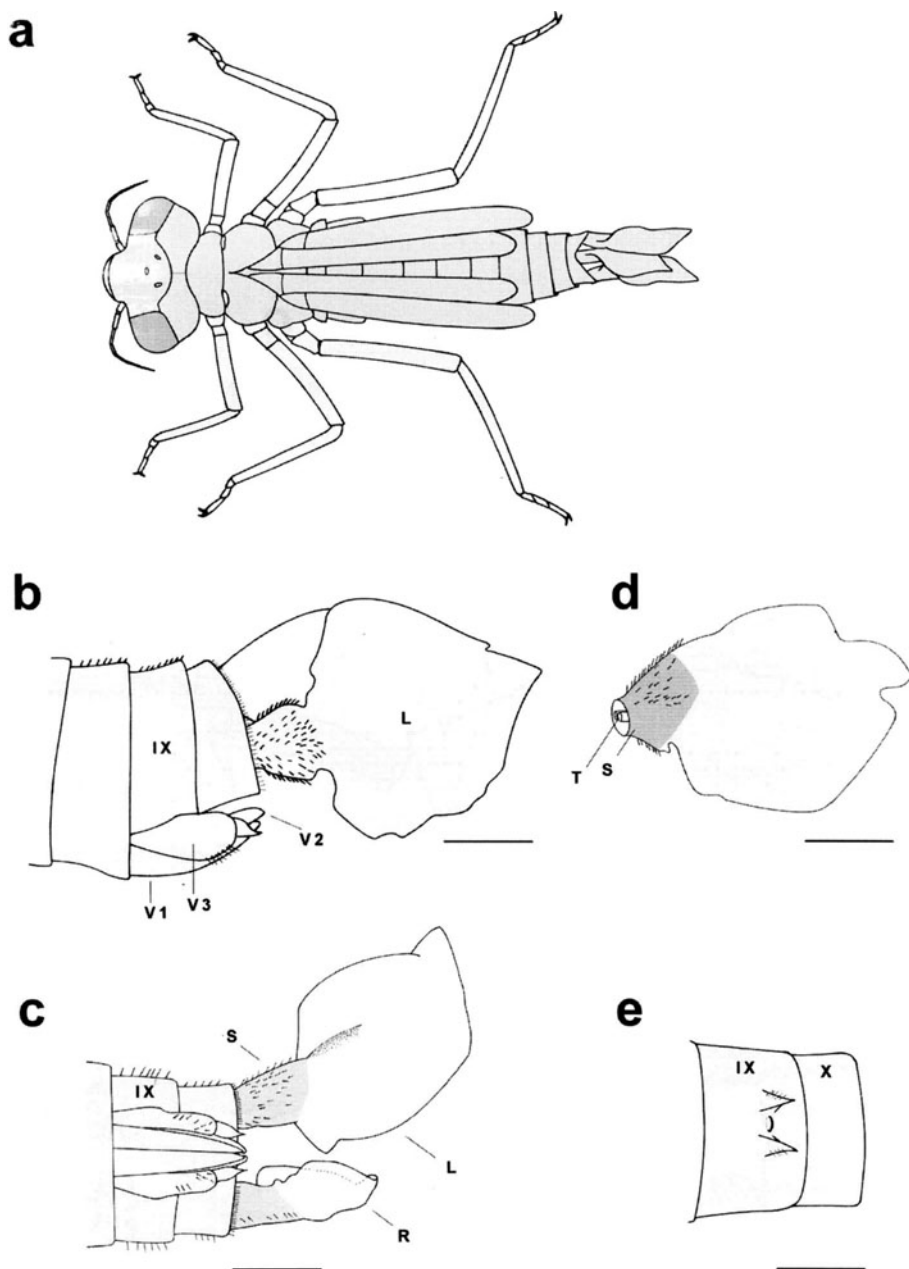


Figure 2. Last stadium larva of *Coryphagrion grandis* – (a) generalized habitus, dorsal view; (b) end of female abdomen, left lateral view; (c) end of female abdomen, ventral view; (d) median caudal appendage; (e) male gonopods, ventral view. Scale bar for (a): 5 mm, for (b)-(e): 0.5 mm. L = lateral caudal appendage; R = regenerated caudal appendage; S = sclerotised stalked base of the caudal appendage; T = trachea; V1, V2, V3 = valvula 1,2 and 3; IX = S9.

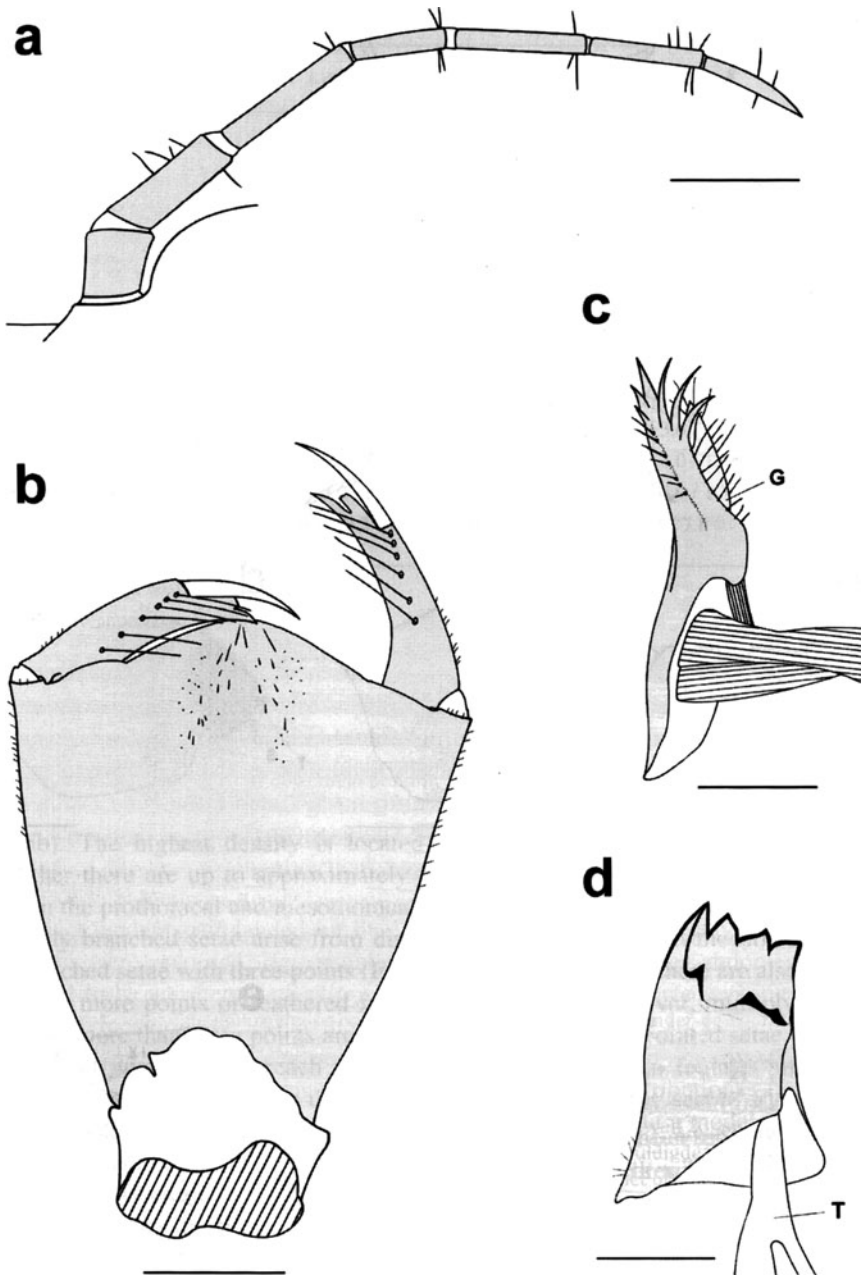


Figure 3. Last stadium larva of *Coryphagrion grandis* – (a) right antenna; (b) prementum, dorsal view; (c) right maxilla, lacinia and galea (G); (d) mandibel with adductor tendon (T), inner side. Scale bar for (a), (c), (d): 0.5 mm; for (b): 1 mm.



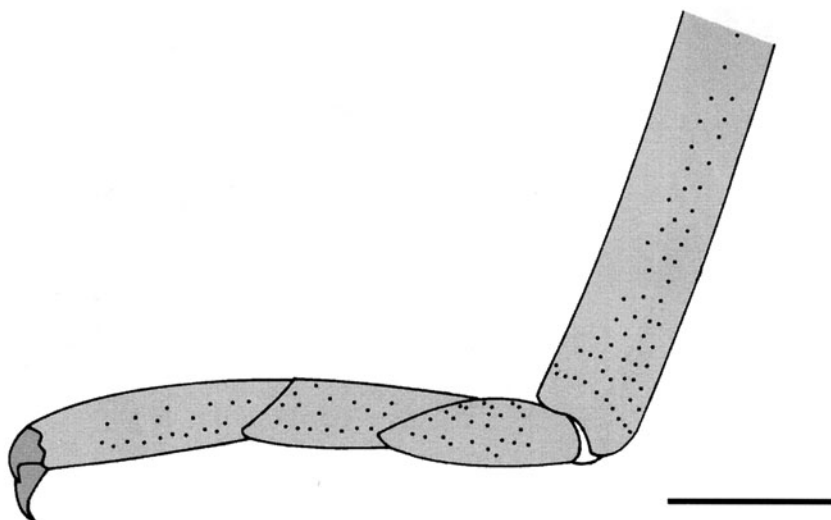
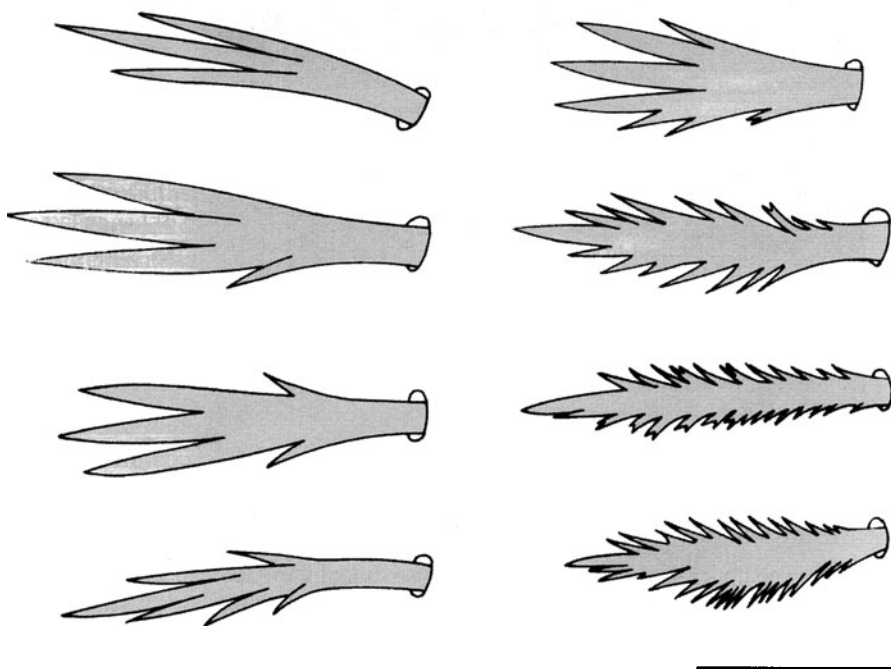
**a****b**

Figure 4. Last stadium larva of *Coryphagrion grandis* – (a) branched setae pattern on the inner side of tibia and tarsi, foreleg, ventrolateral view; (b) different types of branched and feathered setae. Scale bar for (a): 0.5 mm, for (b): 50  $\mu$ m.

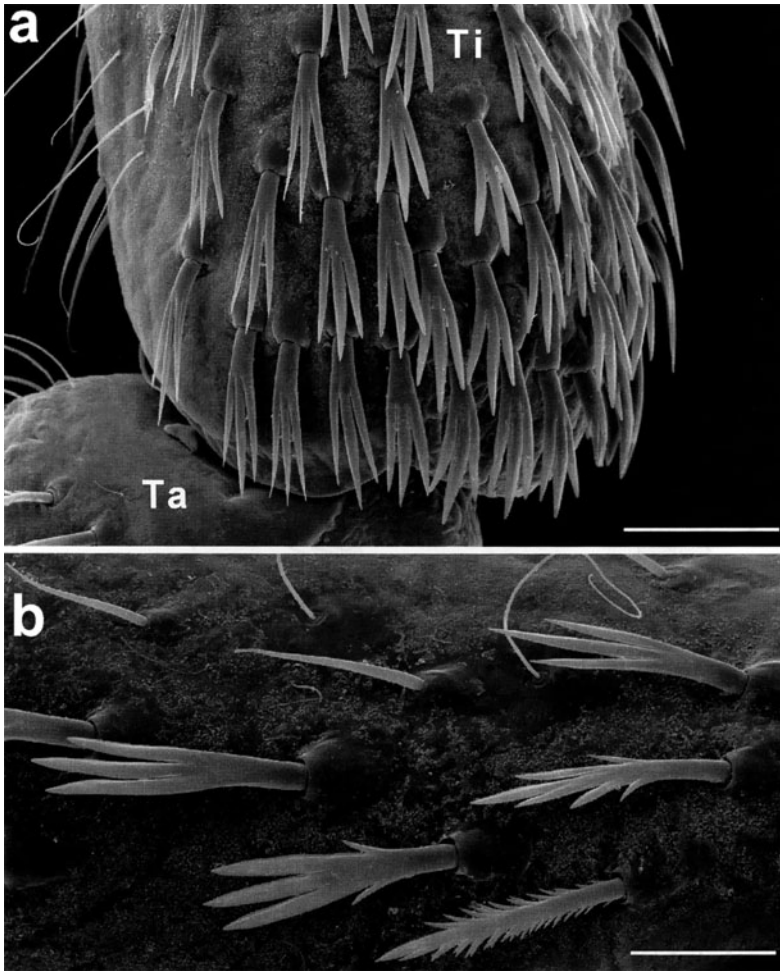


Figure 5. Last stadium larva of *Coryphagrion grandis* – (a) distal end of tibia (Ti) and proximal end of tarsus 1 (Ta), foreleg, ventrolateral view; (b) different forms of setae on tarsus 1, ventrolateral view. Scale bar for (a): 100  $\mu\text{m}$ , for (b): 50  $\mu\text{m}$ .

*C. grandis* larvae under 4 mm in length (excluding caudal lamellae) were usually found floating upside down under the watersurface (Fig. 7). Larger larvae were often sitting on leaves or along the side of the treehole, with their caudal lamellae hold spread out horizontally on the water surface. If approaching a treehole carefully it was very easy to spot either the floating larvae or the caudal lamellae, which was a good indicator of presence or absence of *C. grandis* larvae in that hole.

Larvae kept in captivity spent most of the time sitting either on the ground of

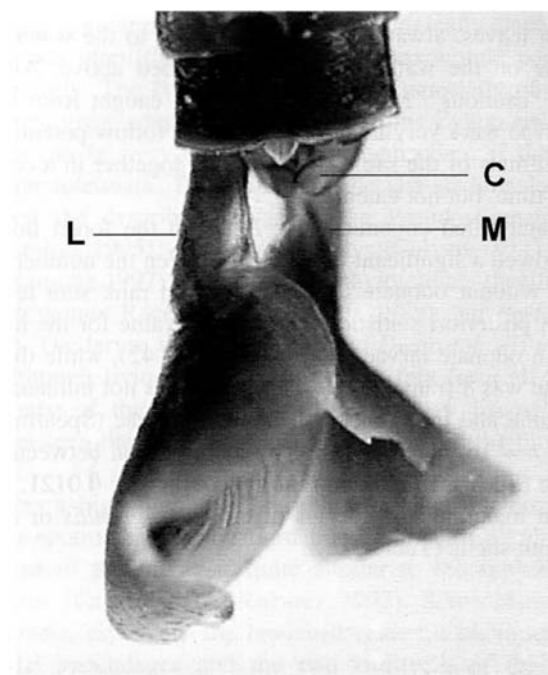


Figure 6. Last stadium larva of *Coryphagrion grandis* – caudal appendage; M = median, L = lateral caudal appendage, C = cercus.



Figure 7. *Coryphagrion grandis* larvae, body lengths 3.5 and 2 mm, floating upside down under the water surface, Shimba Hills, Kenya, 15 April 2001.

the container or on leaves, always in a short distance to the water surface, spreading the caudal lamellae on the water surface as described above. All movements were extremely slow or “cautious”. Mosquito larvae were caught from the sitting position. If the dragonfly larvae were very hungry, they would follow potential prey through the container. If two animals of the same size were put together in a container, one would be killed in a short time, but not eaten.

A survey of water filled coconut shells lying on the forest floor of the Gongoni Forest (Table 3) showed a significant difference between the number of mosquito larvae in shells with and without odonate larvae (Wilcoxon rank sum test,  $n = 5$ ,  $m = 11$ ,  $z = 3.0$ ,  $p < 0.01$ , a posteriori statistic). The median value for the number of mosquito larvae in shells with odonate larvae was 29 (range 17-42), while the median value for shells without larvae was 8 (range 4-22). This result was not influenced by a correlation between water volume and the number of mosquito larvae (Spearman rank correlation coefficient:  $-1.857$ ;  $n = 16$ ,  $p = 0.491$ ) nor by a correlation between water volume and the dragonfly larvae (Spearman rank correlation coefficient:  $0.0121$ ;  $n = 16$ ,  $p = 0.965$ ). With one exception maximal one species of either *C. grandis* or *H. scabrifrons* was present in the coconut shells (Table 3).

## Discussion

Phytotelmata are often described as oxygen-deficient (e.g. Corbet 1983), although there is a strong difference between the various types of phytotelmata. Water in bromeliads has a surprisingly high oxygen saturation of 33% (Diesel & Schubart 2000), if compared to the oxygen contents measured in the dendrolimnetic treeholes under a closed canopy in the Shimba Hills (Table 1). The oxygen contents measured in this study were much lower than contents indicated as “normal environmental range” for the pond species *Lestes disjunctus* Selys (cited in Corbet 1999: 84-85). Dendrolimnetic phytotelmata have a permanently low oxygen content and are probably one of the most oxygen-deficient habitats utilized by odonate larvae. Conductivity and pH are very similar to the ones measured by Kitching (1986), including the high variability of the conductivity. The latter is highly dependent on the amount of detritus and eventually dead organism, e.g. in one treehole a rotting freshwater crab was found on the bottom.

The caudal appendages of *Coryphagrion grandis* larvae, stalked at the base and spatulate distally, and the behaviour to hold them most of the time close to the water surface are most probably adaptations to the oxygen-deficient microhabitat. Although having no evidence, we postulate that the caudal appendages of *C. grandis* are used as gills for respiration. The behaviour of the *C. grandis* larvae supports the respiratory function of the caudal appendages. This behaviour is similar to that described from larvae of Pseudostigmatidae from Central America. Fincke (1992b) observed pseudostigmatid larvae under 7 mm in length often resting near the surface of the water, whereas medium to large larvae were usually found in deeper water, with their caudal lamellae held near the water surface.

Due to convergent evolution, e.g. the modified leaf-like caudal appendages, most

phytotelmata-dwelling zygoteran species are morphologically similar. The form of the caudal appendages was often thought to reflect the taxonomic position, but this has to be examined carefully. The functional morphology specially of caudal appendages might have undergone great adaptive radiation and thus Zygoptera larvae of different families and genera can be very similar among themselves, if they inhabit identical microhabitats like phytotelmata. The habitus of the last stadium larvae of *C. grandis* reminds strongly on the described larvae of the Pseudostigmatidae *Mecistogaster ornata* Rambur (Ramirez 1995), *M. modestus* Selys (Calvert 1911) and *Megaloprepus caerulatus* Drury (Ramirez 1997), but also of the phytotelmata-dwelling Coenagrionidae *Leptagrion fernandezianum* Rácenis (De Marmels 1985) and *Pericnemis triangularis* Laidlaw (Orr 1994). The larvae of the coenagrionid *Diceratobasis macrogaster* (Selys) (Westfall 1976), although living in phytotelmata, differs from all mentioned species, specially in the shape of the caudal appendages and is discussed to represent an intermediate step between the “normal” Coenagrionidae and the phytotelmata dwellers (Ramirez 1997).

*C. grandis* shares a high number of morphological characters next to the caudal appendages with the neotropical Pseudostigmatidae, which are all phytotelmata dwellers as well. The habitus of the larvae is quite similar to the typical *Megaloprepus* or *Mecistogaster* habitus (Calvert 1911; Ramirez 1997). Some characteristics found in the larva of *C. grandis*, especially the branched setae on tibiae and tarsi, the unique shape of the caudal appendages and the two end-teeth of the labial palpi differ not from known larvae of the Pseudostigmatidae. These features are constant in all known Pseudostigmatidae larvae, but variable in phytotelmata-dwelling Coenagrionidae, indicating a convergent development in the latter.

The similar larval characteristics between *C. grandis* and the Pseudostigmatidae may be synapomorphies of a monophyletic group consisting of Pseudostigmatidae plus Coryphagrionidae (cf. Bechly 1996) or of the Pseudostigmatidae including *C. grandis*. According to this interpretation *C. grandis* and the Pseudostigmatidae share the following common features as synapomorphies: wings very long and slender; nodus in a extremely basal position, convergent to Perilestidae and Platystictidae; very elongated and slender abdomen; exophytic oviposition in phytotelmata. It seems that the larval characters – branched setae, form of the caudal appendages – support the monophyly of Pseudostigmatidae plus *Coryphagrion*, just as the feeding method, feeding on prey/spiders in spider webs. Based on actual knowledge of larval morphology, adult morphology, ecology and behaviour of the family Pseudostigmatidae, the authors consider *C. grandis* as at least closely related to the Pseudostigmatidae. It might either be a monophyletic sistergroup or belong within the Pseudostigmatidae.

In both cases, this is of high biogeographic significance. *C. grandis* would then be an afrotropical relict of Gondwana (Goldblatt 1993) which was separated from the neotropical Pseudostigmatidae about 100 million years ago and remained surprisingly similar to the latter. The occurrence in East Africa and not in West Africa, as one would expect, can be explained with climatic stability in Eastern Africa and the changes of forest cover in Africa. The coastal forests of Eastern Africa are considered to be partial relicts of the former pan-African tropical forest (Fjeldsa et al. 1997; Fjeldsa & Lovett 1997). These forests are believed to have been climatically stable during Ice Age

periods unlike the forests in West Africa, based on estimates of the water temperature of the Indian and the Atlantic Ocean. West African *Coryphagrion* populations might have become extinct during colder periods, which resulted in a decline of rain and therefore of forest in West and Central Africa (Clarke 2000). Additionally during cooling periods at the equator much of tropical Africa must have cooled to below the tolerances of tropical stenothermic species, which might have led to random extinctions in the African rain forests (Colinvaux 1993: 494).

A comparative study on adult morphology of *C. grandis* and neotropical Pseudostigmatidae will be published by the authors in due course.

One interesting morphological feature of the larva are the branched setae (Figs 4, 5). The exact function of branched setae is not known yet as well as possible advantages or disadvantages in comparison to simple pointed setae. Branched setae are also found on the inner side of the tibiae of *Coenagrion intermedium* Lohmann (Battin 1991). Unfortunately, there is not any reliable information about the distribution of this feature in Odonata. Therefore the phylogenetic relevance of branched setae remains unclear for the lack of information on this character. Possibly the existence of branched setae and the setae pattern may be used for systematic analyses in the future. Many other larval features are extremely variable, for example the number of palpal setae. Such characters have no phylogenetic value.

The finding of usually not more than one surviving larvae in an average sized tree hole (Tables 3, 4) corresponds to observations reported from other species breeding in phytotelmata as well (e.g. Diesel 1992; Fincke 1992a, 1992c; Orr 1994) and is presumably a result of cannibalism. Unlike the reported cannibalism of *C. grandis* within one cohort, Lounibos et al. (1987) noted co-occurring larvae of *Leptagrion siqueirai* Santos in bromeliads holding 50-100 ml fluid. But these were of the same size class and he postulated cannibalism only by older conspecifics.

## Acknowledgements

The first author wishes to thank following people and institutions for help and support: Richard Bagine (Kenya Wildlife Service), Lucie Rogo (International Centre for Insect Physiology and Ecology, Nairobi), Wanja Kinuthia (National Museum of Kenya), the Warden in Charge and the staff of Shimba Hills NP and David Goodger (Nature History Museum, London). The A.F.W. Schimper-Stiftung, the German Scientific Research Foundation (DFG), the International Dragonfly Foundation (IDF) and the German Federal Ministry of Science (BMBF, BIOLOG Programme) are thanked for funding the work. Sabine Griesbach is warmly thanked for her help and hospitality in Nairobi.

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